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Predators and parasitoids of egg sacs of the widow spiders, *Latrodectus geometricus* and *Latrodectus hesperus* (Araneae: Theridiidae) in southern California

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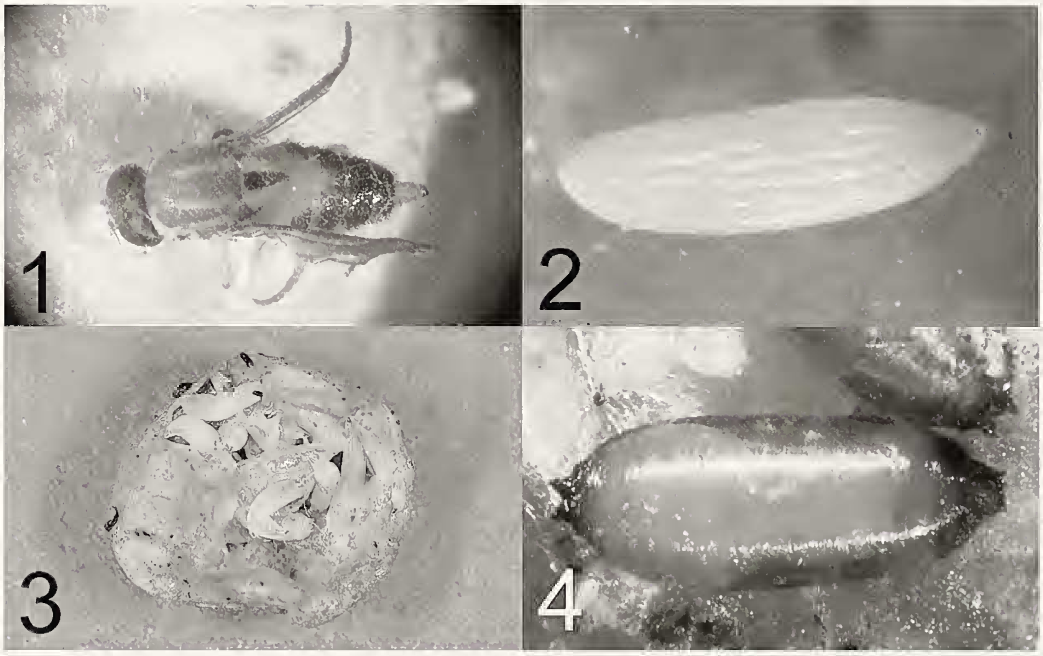
Abstract. The brown widow spider, *Latrodectus geometricus* C. L. Koch 1841, is non-native to North America and has experienced an explosive range expansion in the first decade of the 21st century. Previously restricted to peninsular Florida, it is now well established in the southeastern United States and southern California. In southern California, brown widow spiders have become ubiquitous around urban homes and are well known to the general public because of their high numbers and distinctive spiked egg sacs. Several insects attack egg sacs of the native western black widow, *L. hesperus* Chamberlin & Ivie 1935, as either parasitoids or egg predators. We investigated whether and to what degree these insects would attack brown widow egg sacs. We dissected 3,739 brown widow egg sacs finding evidence of the chloropid fly, *Pseudogaurax signatus* (Loew 1876) in 2.0% and wasp parasitoids in 0.4% of the sacs. For comparison, we also dissected 263 western black widow egg sacs with *P. signatus* showing a higher level of predation (6.1%). Other brown widow sac inhabitants included larvae and adults of dermestid beetles, psocids, and lepidopterans, which are probably scavengers or incidental occupants. The overall impact of the recorded predators and parasitoids is too low to explore the possibility of a biological control program. Additionally, due to the relatively low number of predators/parasitoids in brown widow egg sacs and the entanglement of small arthropods on the outer surface, we speculate that the spiked egg sac surface might serve as an effective barrier to most predators and parasitoids.

Keywords: Black widow, brown widow, egg predator, parasitism, *Pseudogaurax*

The brown widow spider, *Latrodectus geometricus* C. L. Koch 1841, was originally described from Colombia, South America (Lotz 1994) and is not native to North America. However, it is probably native to Africa where it has widespread distribution and has its closest sister species (Garb et al. 2004). It was first recorded in North America in Florida in 1935 (Pearson 1936) and was isolated in the peninsular portion of the state for decades. Inexplicably, in the first decade of the 21st century, an explosive population expansion occurred such that by 2011, it was well established in the southeastern United States from Texas to South Carolina (Brown et al. 2008; Vincent et al. 2008), with specimens recently reported from North Carolina (pers. comm. to RSV). In southern California, the brown widow was first discovered in Los Angeles County in 2003 (Vincent et al. 2008), where it is now found in urban areas from San Diego to the western portions of Los Angeles County and east to western Riverside and San Bernardino Counties. In less than a decade, the brown widow has become one of the most common and easily recognizable spiders in urban southern California, such that the general public is both well aware of its presence and can usually accurately identify the spider or its egg sacs on their property.

The egg sac of the western black widow, *Latrodectus hesperus* Chamberlin & Ivie 1935, is known to be attacked by insect parasitoids and egg predators in southern California (Pierce 1942; Kaston 1970). A fly, *Pseudogaurax signatus* (Loew 1876) (Diptera: Chloropidae), (Fig. 1) lays its eggs (Fig. 2) on the outside of western black widow egg sacs; maggots hatch and push their way through the fibers of the sac to the inside where they feed upon multiple eggs and develop inside the sac (Kessel & Kessel 1937; Barnes et al. 1992). As they near pupation, the larvae (Fig. 3) thin the inside surface of the sac and pupate (Fig. 4), with emerging flies pushing their way through the thinned silk walls (Kessel & Kessel 1937). In contrast, the tiny wasp, *Baeus latrodecti* Dozier 1931 (Hymenoptera: Platygastridae s. l.) is an efficient egg endoparasitoid. The adult female chews its way into western black widow egg sacs and lays one egg per spider egg; within individual egg sacs, parasitism rates can approach 100% (Pierce 1942). *Baeus latrodecti* was discovered and reared in southern California for use in biocontrol programs in Hawaii against *Latrodectus mactans* (Fabricius 1775); however, it was collected in only one isolated area in southern California (Pierce 1942). The females are 0.75 mm long and wingless, which may reduce their ability to disperse over wide distances, at least in southern California. From western black widow spider egg sacs in the San Francisco Bay area, Herms et al. (1935) found *P. signatus* and *B. latrodecti*, as well as an ichneumonid wasp, *Gelis* sp.

Pemberton & Rosa (1940) report that attempts to rear *B. latrodecti* on *L. geometricus* eggs failed; however, in a later study the same authors document an undescribed eurytomid wasp that was parasitizing brown widow egg sacs in Hawaii (Pemberton & Rosa 1946). Other eurytomid wasps that parasitize brown widow egg sacs include *Philolema* (=*Eurytoma*) *arachnovora* (Hesse 1942), in Jamaica (Baerg 1954) and *Philolema latrodecti* (Fullaway 1953) in Florida (Brown et al. 2008). Brown et al. (2008) note that they collected chalcidoid wasps in brown widow egg sacs, although they did not list the



Figures 1–4.—Chloropid fly, *Pseudogaurax signatus*. 1. Adult, removed from alcohol for photo, body length of 3 mm; 2. Egg, 0.55 mm long; 3. Larvae in a western black widow egg sac. This sac was opened, the larvae discovered and then photographed. In normal situations, the larvae remain inside the closed egg sac to pupate, and the adult flies emerge from the sac; 4. Pupa, 3.66 mm long.

location of collection. In southern Africa, Hesse (1942) lists *P. arachnovora* and adds *Gelis* (=*Pezomachus*) *latrodectiphagus* (Hesse 1942) as parasitoids of the African widow species, *L. indistinctus* O. P.-Cambridge 1904. In Australia, egg sacs of the red-back widow, *L. hasselti* Thorell 1870, are infested or attacked by two species of eurytomid wasps, one ichneumonid wasp, and a mantispid (Austin 1985).

Because the brown widow spider is a newly established non-native species, we were interested in determining the response of parasitoids and egg predators in southern California to this new potential host. This study was undertaken to determine 1) whether parasitoids and predators of western black widow eggs will attack brown widow egg sacs; 2) if so, to what level do they infest brown widow egg sacs and 3) can any of these egg predators or parasitoids be potential candidates for developing a natural biological control program to reduce or modulate the non-native brown widow populations?

METHODS

The egg sac of the brown widow is readily recognizable as a small sphere covered with silk spicules such that it has been described as looking like a large pollen ball or a World War II harbor mine (Fig. 5). In addition, it is common to find several to dozens of egg sacs in one location, hence increasing their conspicuousness to the average homeowner. Therefore, we were able to solicit egg sacs from homeowners throughout southern California, generating large numbers of sacs from a broader area than we would have been able to collect ourselves.

The project ran from May to October 2011. It was promoted on the Center for Invasive Species Research website at the University of California, Riverside. Because part of this study was funded by Orange County, we were allowed access to various county facilities (parks, zoos, horticultural facility, historic ranch) for searches. One of us (JNK) alerted the Orange County Master Gardeners to our project, requesting permission to search their property and gardens. In addition, articles in three local newspapers (Los Angeles Times, Orange County Register, Riverside Press-Enterprise), as well as interviews with two Los Angeles television stations and a radio station, instigated a great outpouring of specimen submissions by the general public. We also collected egg sacs of *L. hesperus* to provide a comparison to those of *L. geometricus*. Regarding the native western black widow egg sacs, 62% of the total were collected from two adjoining properties in Moreno Valley, California that were zoned for horses (i.e., there were barns with abundant western black widow habitat in xeric chaparral landscaping).

We pulled egg sacs open with fine forceps under a microscope and assigned the contents to various categories (Table 1). Minor overlap between some categories required us to establish sorting rules; that is, if an egg sac had about equal numbers of unhatched and cast shells of hatched eggs, we would place it in the Dead, Loose Eggs category but if there were just a few unhatched eggs but most hatched, we considered it to be in the Successful Hatch and Emergence category. In the category where egg or spiderling death was recorded, we could not differentiate among those that were dead due to infertility, insecticide, heat (ambient or encountered during shipping) or inability to chew an exit hole to escape. We recorded all instances of parasitism of egg sacs. Egg sacs that had live eggs or first or second instar spiderlings were placed in individual vials for later inspection in case there were still developing parasitoids or egg predators not visible amongst the hundreds of eggs. (In reality, only one of about 300 egg sacs treated this way resulted in the discovery of an egg predator.) We examined all egg sacs, no matter how old, because if parasitoids/predators were ever present therein, the evidence would still be detectable.

Figure 5.—Spiked egg sacs of the brown widow spider.

Most often the presence of *P. signatus* was determined by empty pupal cases. Although there is no key to pupal cases for this genus, of those sacs from which live flies emerged, all flies keyed out to *P. signatus* using Sabrosky (1966), and the empty pupal cases from other egg sacs matched those from which flies emerged. Hence, we assumed that there was only one species of fly preying on *Latrodectus* eggs and that all were *P. signatus*. Only two *Pseudogaurax* species exist in the United States with *P. anchora* (Loew 1866) being limited to the eastern U. S. and *P. signatus* having widespread distribution throughout the southern portion of the country (Sabrosky 1966). Hall (1937) mentions that *P. signatus* is found anywhere that *L. mactans* is found. (Note: in 1937, *L. mactans* was the blanket name used for several current *Latrodectus* species in the United States including *L. hesperus*.)

Egg sacs containing fly pupae or their empty cases were treated as follows to separate and harvest pupal cases that were intertwined in the interior silk of the egg sac. An egg sac was dipped into alcohol to reduce hydrophobicity of the silk and then placed into a small petri dish where it was covered with a small amount of commercial bleach (6% sodium hypochlorite), which dissolves spider silk in a few minutes (Vetter et al. 1996). The pupal cases were then easily extracted from the dissolved silk mass, counted, and placed in individual vials with alcohol and an identification label.

To understand the potential reproductive success of *P. signatus*, we counted the number of eggs in sacs for the brown widow (n = 30) and the western black widow (n = 10). We measured diameters of 40 eggs of each species with a Leica MZ16 microscope fitted with an ocular micrometer. Only field-collected egg sacs were used, so that the numbers that were generated would represent the productivity of naturally feeding females.

Rates of infestation for western black and brown widows were compared with an R × C contingency test of independence. The number of fly pupal cases and eggs per sac for each species was analyzed with a Welch's T-test for unequal variance. A comparison of the eggs per egg sac was analyzed with a two-sample t test (Statistix 9, 2009).

RESULTS

We dissected 3,739 brown widow and 263 western black widow egg sacs. Table 1 lists the contents of the sacs. The brown widow egg sacs showed an overall infestation rate of 2.38% including the chloropid fly, *P. signatus* (1.98%), parasitized eggs or empty capsules of small wasps (0.24%) and pupae or empty pupation capsules of larger wasps (0.16%), whereas the western black widow sacs showed an infestation rate of 6.1%, composed solely of *P. signatus*. Most of the wasp pupal capsules were empty, so it was not possible to assign predation/parasitism rates to specific species or to be assured that only one species was involved. The larger wasp pupal capsules were typically found attached to the outside wall of the brown widow egg sac or wedged between multiple spider egg sacs. It was assumed that these larger capsules represented wasps that were feeding on brown widow eggs, however it is possible that they merely used the egg sacs as a pupation substrate after feeding on another arthropod host nearby. Of the few wasps that emerged, wasp taxonomists identified males and females of *Aradophagus fasciatus* Ashmead 1893 (Platygastridae s. l.), and one male of *Gelis* sp. (Ichneumonidae). A lepidopterist colleague identified the Florida pink scavenger moth, *Pyroderces badia* (Hodges 1962) (Cosmopterigidae).

When comparing the two spider species for the overall degree of *Pseudogaurax signatus* pupae presence, the western black widow had a significantly greater infestation rate than did the brown widow (G_1 = 13.36, $P < 0.005$). There was no statistical difference between the average number of fly pupae in western black widow egg sacs (10.63 ± 12.85, range 1–39, n = 16) and brown widow egg sacs (4.79 ± 4.39, range 1–25, n = 70) ($T_{15.8} = -1.79$, P = 0.10). (Because of the 2:1 ratio of fly pupae in black:brown widow egg sacs, we were surprised that this difference was not significant, but realized that it may have been due to low black widow sample size and great variance. In subsequent hypothetical calculations, assuming the same mean and variance for both spider species but increasing the black widow sample size to 30 or more, the

Table 1.—Results of the contents (by percentage) from dissections of 3,739 brown widow and 263 western black widow spider egg sacs for various categories.

	Brown widow	Western black widow
Fly Egg Predators or Wasp Parasitoids		
Fly pupae or empty pupal cases	1.98	6.08
Wasp parasitized eggs or empty pupal cases	0.40	0.00
Dead Material		
Dead, loose eggs (with any other content)	17.54	14.07
Dead spiderlings	4.23	2.66
Clump of dead, un-separated eggs	3.99	0.76
Live Material		
Live, viable-looking eggs	5.11	4.56
Pale, newly hatched 1st instars	2.41	0.38
Live mobile spiderlings	6.90	1.14
Egg sac empty, spiderlings dispersed		
Successful hatch and emergence	50.60	64.26
Sac scavenged, no remnant silk or exuviae	3.24	2.28
Other		
Dermestid beetle evidence	0.72	3.80
Amorphous blackened remnant (fungus?)	2.30	0.00
Other	0.56	0.00

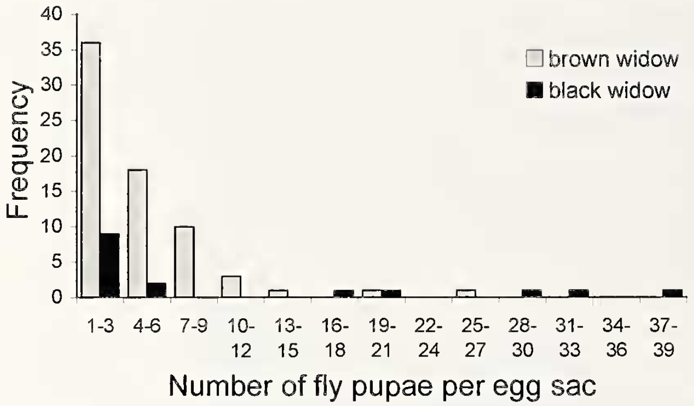


Figure 6.—The number of fly pupae found in brown and western black widow spider egg sacs.

difference would have been statistically significant.) The distribution of fly pupae was somewhat bimodal for western black widows with either few (< 6) or many (> 18) pupae found per sac; brown widow sacs produced few pupae (Fig. 6). The western black widow had a significantly greater number of eggs per sac (276.1 ± 97.2, range = 126–386, n = 10) than the brown widow (143.7 ± 61.6, range = 57–286, n = 30) (t_{38} = 4.68, $P < 0.0001$). Average egg diameters (and volumes) were 1.059 ± 0.026 mm (0.622 mm^3) for western black widows and 0.915 ± 0.023 mm (0.401 mm^3) for brown widows. Multiplying average egg volume by the number of eggs yields 171.7 mm^3 of egg volume in an average western black widow egg sac, compared to 57.6 mm^3 in an average brown widow sac, a ratio of 3.2 times more black than brown widow total egg volume available for egg predation.

In addition to the above-mentioned insects, we found evidence of other arthropods (Table 1), mostly scavengers or incidental occupants in the egg sacs. We found dermestid beetle larvae or their cast skins, empty lepidopteran pupal cases, and psocids. Dead Argentine ants, *Linepithema humile* (Mayr 1868), were occasionally found stuck to the outside of the brown widow egg sac and tangled in the loose threads among the silk spikes. Two brown widow egg sacs contained 74 and 15 ants of the genus *Monomorium* that had crawled inside, were dead and tangled in the inner sac silk. Interestingly, we found the shed skins of salticid spiders inside two empty sacs, indicating that they sought the interior of the sac as a safe refuge during molting.

We found a large number of egg sacs of both *Latrodectus* species that had unhatched, discolored and shrunken eggs, or dead first and second instars (Table 1). For the older spiderlings, it appeared that some of this resulted because of the inability of the spiderlings to chew an exit hole. In others, some sacs were completely empty inside; all evidence of eggs, shed skins and the inner layer of silk was gone. These empty sac walls often had a large (6 mm) hole as opposed to the small (0.8 mm) hole that the spiderlings chew to exit the sac. Occasionally, we found evidence of dermestids in these sacs, although a 6 mm hole is much larger than necessary for a dermestid to enter and exit.

DISCUSSION

The current study examined thousands of brown widow egg sacs, virtually canvassing the entire southern California range where the spider currently is known to exist. The chloropid fly, *P. signatus*, infests brown widow egg sacs, albeit at a very low level. Additional parasitoids were found in extremely low frequency and, therefore, have insignificant potential for a biocontrol effect on brown widow populations. The one moth specimen that was identified (*Pyroderces badia*) may actually be an egg predator in addition to being a scavenger, as its common name indicates; in Australia, Austin (1977) documented *Pyroderces* (=*Anatrachyntis*) *terminella* Walker 1864 as an egg predator of the nephilid spider, *Nephila edulis* (Labillardière 1799). We saw no evidence of the tiny platygastrid wasp, *B. latrodecti*, attacking either spider species.

Pseudogaurax signatus was found in egg sacs throughout the southern California range of the brown widow, even though climate varies from the reliably temperate and humid coastal regions (such as La Jolla, Laguna Beach) to the hot, dry inland areas (Riverside, Redlands) where temperatures routinely exceed 40° C in summer. This is similar to the findings by Pierce (1942) where he reported this species in western black widow egg sacs throughout the Los Angeles Basin as well as from the desert cities of Coachella and Blythe where summer temperatures routinely reach 45° C and can approach 50° C on occasion. This fly also infests egg sacs of araneid and tetragnathid spiders (Pierce 1942; Barnes et al. 1992). Austin (1985) lists 26 spider species in eight families that are attacked by chloropid flies of the genera *Gaurax* or *Pseudogaurax*.

In our study, 6.1% of western black widow egg sacs were infested with *Pseudogaurax signatus*. Comparing this to other studies, *P. signatus* infested 40% of western black widow egg sacs in the San Francisco Bay area (Kessel & Kessel 1937) but only 4.8% in southern California (Pierce 1942). The low infestation rate of the brown widow egg sacs (1.98%) confirms that employing this fly for biological control is not promising in southern California. This is somewhat surprising given the great number of brown widow egg sacs that were available for predation compared to the lower number of western black widow sacs. However, there are many factors, both physical and chemical, that are involved in determining whether a parasitoid or predator can effectively switch hosts, a consequence of the tight evolutionary relationship between the species. Yet *P. signatus* has a somewhat eclectic host range, using several spider families, and was able to occasionally utilize the non-native brown widow to some degree due to its recognition of a species in the *Latrodectus* genus. It might be interesting to revisit this relationship in five to ten years to see if *P. signatus* is able to increase its use of brown widow egg sacs for larval development over time. In contrast, host specificity for endoparasitoids may be more stringent. For example, even though the wingless wasp, *B. latrodecti*, is a very efficient parasitoid on *L. mactans* (Pemberton & Rosa 1940) and *L. hesperus* (Pierce 1942), it cannot be reared on *L. geometricus* (Pemberton & Rosa 1940). One additional avenue to pursue would be to examine the contents of mud-dauber wasp nests for brown widow spiders because immature black widows are favored prey of some species of the larger wasps (Irving & Hinman 1935; Rau 1935; Kaston 1970).

In contrast to the low levels of parasitism or egg predation, natural death of eggs inside the egg sac may account for much greater mortality. Many egg sacs contained eggs that never hatched, instead being dry and shriveled (Table 1). Baerg

Figure 7.—Spiked egg sac surface of the brown widow spider (top) and the smooth egg sac surface of the western black widow spider (bottom).

(1954) mentions that a large percentage of brown widow egg sacs similarly did not develop during the drought season in Jamaica. Considering the Mediterranean climate in southern California, the hot inland temperatures might play a role in reducing brown widow populations or not allowing them to become established. However, the coastal regions are reliably cool and humid, which might encourage brown widow populations.

A very rewarding aspect of this study was the enthusiasm of the southern California homeowners in submitting egg sacs and allowing us access to their property. Piles of boxes came through the mail every week for most of the summer, and sometimes a homeowner spent several dollars to mail just one egg sac. This was similar to the experience of Pierce (1942) when he used the media to alert the Los Angeles public to the need for black widow egg sacs. In his article, Pierce acknowledges the help of many high school students who were critical in handling the large volume of western black widow egg sacs that were submitted. (One of these students was Evert Schlinger who eventually became Professor of Entomology at the University of California, Berkeley, researched acrocerid flies that parasitize spiders and served as major professor for many arachnology students including the second author of this paper.) Many times in our study during the collections at a home, the homeowner followed us around his or her yard as we collected, frequently pointing out spots where brown widows or their egg sacs had been seen. This was a rare, exceptional outreach moment where homeowners interacted with scientists and were both excited and pleased to contribute to a tangible, scientific study that might benefit them.

Egg sac construction may be influenced by the arms race of the spider host attempting to thwart attacks from parasitoids and predators, who in turn attempt to circumvent the host's defenses (Austin 1985). The two widow species had different infestation rates, which has instigated future research regarding the function of silk spicules on the surface of the brown widow egg sac. From the observation of small ants stuck to the outside of a sac and the significantly lower infestation rate of the brown widow sacs as compared to the western black widow, we postulate that the silk surface of the brown widow sac may act as an anti-predator/parasitoid defense. In addition to the silk spikes, there are strands of silk loosely traversing among the spikes. Small wasps might get entangled in or be deterred by the spikes and surrounding silk when they attempt to oviposit on or in the sac, whereas this seems less likely with the smooth surface of the western black widow egg sac (Fig. 7). *Pseudogaurax signatus* lay their eggs flat on the surface of black widow saes; possibly the rugged surface of the brown widow egg sac makes this a more difficult task or undesirable place for the fly egg predators to oviposit. Alternately or additionally, the spiked egg sac surface might entangle or delay newly hatched maggots that are looking for an entry point into the sac. The different infestation rates could also have been influenced by the fineness of the silk weave of the sacs. Brown widows are smaller than black widows, with brown widows possibly weaving a finer mesh, which makes it difficult for the *P. signatus* larvae to push their way inside the sac.

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